Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters

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ABSTRACT: Seabirds concentrate nutrients from large marine areas on their nesting islands. The high nutrient load may cause runoff into surrounding waters and affect marine communities in similar ways to those reported from marine fertilization experiments. In order to test if cormorant colonies affect algae and invertebrates in surrounding coastal waters, we collected *Fucus vesiculosus* fronds, its epiphytic algae, and associated invertebrate fauna near abandoned and active cormorant nesting islands as well as reference islands without nesting cormorants in the Stockholm archipelago in the northern Baltic Sea, Sweden. First, we showed, with $\delta^{15}N$ analyses, that ornithogenic nitrogen provided a significant nitrogen source for algae and invertebrate consumers near islands with high nest density. Second, the nitrogen and phosphorus content of algae near active cormorant islands with high nest density was elevated, and epiphytic algae increased relative to *F. vesiculosus*. Third, 3 of 5 invertebrate taxa (*Jaera albifrons, Gammarus* spp., and Chironomidae) showed increased biomasses near islands with high nest density; but, contrary to former fertilization studies, only *J. albifrons* increased in abundance compared to reference islands. We conclude that runoff from seabird colonies has a profound effect on primary producers and some consumers in the surrounding water, but only if the colonies exceed a certain nest density. Thus, seabirds not only affect marine communities via top-town forces as commonly assumed, but also via bottom-up forces by concentrating nutrients around their nesting islands. Consequently, seabird islands can be seen as natural fertilization experiments and give important insights to the effects of eutrophication of marine systems.

KEY WORDS: Nitrogen · Stable isotopes · Bottom-up · Eutrophication · Baltic Sea · Cormorants

INTRODUCTION

Seabirds play an important role in marine environments, as predators on marine animals and by concentrating marine nutrients on their nesting islands (Hutchinson 1950, Lindeboom 1984). The high nutrient load on nesting islands may cause runoff into surrounding waters and affect marine communities in similar ways to anthropogenic eutrophication (Golovkin & Garkavaya 1975, Staunton Smith & Johnson 1995). Eutrophication of freshwater systems and coastal waters is a serious global problem threatening services that these aquatic resources provide (Postel & Carpenter 1997, Smith 2003, Rönnberg & Bonsdorff 2004). Algae generally respond to increased nitrogen (N) and phosphorus (P) concentration with increased

biomass and changed species composition, whereas consequences of eutrophication on marine consumers are less known and often difficult to study (Tilman 1982, Grover 1997, De Jonge et al. 2002, Smith 2003, Rönnberg & Bonsdorff 2004). Seabird islands might provide suitable natural experiments to study responses by marine organisms to increased nutrient concentration (Wootton 1991).

The water columns of ponds, lakes, tide pools, and oceans near seabird colonies are often enriched in N (NO_3^-, NO_2^-, NH_4^+, NH_3) and P (PO_4^-) (e.g. Golovkin & Garkavaya 1975, Bosman et al. 1986, Bosman & Hockey 1988, Keatley et al. 2009), and should produce strong positive responses of primary producers (Elser et al. 2007). Many studies also show that fast growing filamentous algae and invertebrate consumers respond

with increasing productivity, biomass, and abundance to nutrient enrichments (Pedersen & Borum 1996, Worm et al. 2000, Worm & Sommer 2000, Kraufvelin et al. 2006, Korpinen et al. 2007, Kraufvelin 2007, Råberg & Kautsky 2008). Similarly, algae and vascular plants near seabird colonies were shown to have increased abundances, growth rates, or nutrient contents (Golovkin 1967, Onuf et al. 1977, Bosman et al. 1986, Bosman & Hockey 1988, but see Wootton 1991). These changes in the primary producers can affect aquatic consumers via bottom-up forces and both increase and decrease consumer abundance as shown for zooplankton (Zelickman & Golovkin 1972), polychaetes (Bosman & Hockey 1986), crustaceans (Wootton 1991, Palomo et al. 1999), chironomids (Michelutti et al. 2009), and fishes (Onuf et al.1977).

Previous studies on the effects of seabird colonies on adjusted marine ecosystems did not combine the power of stable isotope analyses for showing trophic links with data on biomass and abundance responses of algae and invertebrates. In the present study, we aimed to connect both types of data for one specific system by collecting *Fucus vesiculosus* (hereafter *Fucus*) fronds with their epiphytic algae and associated invertebrate fauna in coastal waters surrounding cormorant nesting islands (abandoned islands, active islands with low and high nest densities) and reference (i.e. non-cormorant) islands in the archipelago of Stockholm, Sweden. We focused on bottom-up effects and disregarded possible top-down forces from cormorants, through fish consumption, because cormorants usually forage in a rather large area (1250 km^2) and thus might affect also reference islands (Paillisson et al. 2004, Engström 2001).

In order to investigate which algae and invertebrates utilize avian nitrogen, we first compared the δ^{15}N contents of *Fucus*, its epiphytic algae, and associated invertebrate taxa from the 3 cormorant island categories with the reference islands. We expected enriched δ^{15}N ratios of algae and invertebrates near cormorant islands. Second, we investigated indirectly if cormorants increase the nutrient availability in coastal waters around their nesting island by comparing the P content of algae and the N and P content of algae and associated invertebrates from the same set of islands. Third, we tested if the ratio of epiphytic algae to *Fucus* was increased near cormorant islands and expected, based on previous studies on nutrient enrichment effects in marine systems, increased epiphytic loads in the waters near cormorant islands (Worm et al. 2000, Råberg & Kautsky 2008). Fourth, we investigated if aquatic invertebrates responded to the high nutrient loads around cormorant islands by comparing the abundance and biomass of invertebrate grazers and chironomids from the 3 cormorant island categories with reference islands. Based on previous studies — both nutrient enrichment studies in the Baltic Sea (Kotta et al. 2000, Kraufvelin 2007) and studies investigating the effects of seabirds on aquatic consumers (Bosman & Hockey 1986, Palomo et al. 1999, Michelutti et al. 2009) — we expected increased invertebrate abundances and biomasses near cormorant islands.

MATERIALS AND METHODS

Study site and study species. The study was conducted in late July 2007 and 2008 in the Stockholm archipelago in the northern Baltic Sea, Sweden. The Baltic Sea is a large estuarine system with a narrow connection to the North Sea and no tides. Changes in water level are therefore mainly dependent on regional wind and atmospheric pressure conditions. Furthermore, the Baltic Sea has brackish water, and the salinity in the Stockholm archipelago is about 6 psu. The low salinity enables only a few marine and freshwater species to occur in the Baltic Sea. Eutrophication is one of the major environmental problems in the Baltic Sea, especially in coastal regions, and the main nitrogen sources are rivers and atmospheric deposition (Elmgren 2001, Voss et al. 2006). The yearly nitrogen deposition in the central Baltic Sea was estimated to be 617 mg N m^{-2} yr^{-1} and composed of ~10% organic N and approximately equal amounts of ammonium and nitrate, with an average δ^{15}N = 2.0‰ (Rolff et al. 2008). The yearly phosphorus deposition is much lower averaging 7.3 mg N m^{-2} yr^{-1}, and consists of 20 to 40% organic P (Rolff et al. 2008).

Cormorants *Phalacrocorax carbo* recolonized the Stockholm archipelago in 1994, after hundreds of years of absence, increasing strongly in numbers until 2007 when the population size seemed to have stabilized at about 5200 breeding pairs (Staav 2008, 2009, 2010). From April to August, the cormorants nest in colonies, distributed over about 20 islands across the archipelago (Staav 2008). To illustrate the quantitative flow of nutrients on and around cormorant nesting islands, we used published data on the nutrient content of guano (Fig. 1). Cormorant guano is, as other seabird guano, highly enriched in N and P, but the exact nutrient composition seems to differ between habitats (Marion et al. 1994, Osono et al. 2002). Dry cormorant guano from a French lake was reported to contain 3.3% N and 14.3% P (Marion et al. 1994), whereas the cormorant guano from a Japanese lake was estimated to contain 10.1% N and 9.2% P (Osono et al. 2002). Based on these figures, the per capita deposition from nesting cormorants can be calculated as 4.5 to 11.5 g d^{-1} N and 2.1 to 3.2 g P d^{-1} (Hahn et al. 2007). Assuming a colony
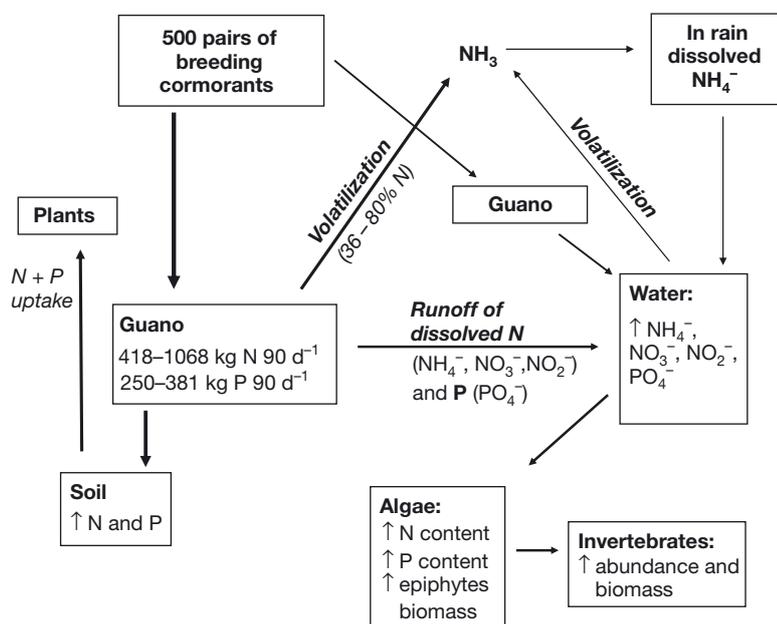
Fig. 1. Conceptual model illustrating the estimated nutrient flows on and around cormorant islands with high nest density (500 nests) and expected changes in nutrient content and biomass of algae and invertebrates in coastal waters. Vertical arrows in boxes denote an increase

with 500 nests and a breeding success of 1.3, this yields a nutrient load of 418 to 1068 kg N and 250 to 381 kg P after 90 breeding days. The principal form of P in fresh guano is PO_4^- (54%; Lindeboom 1884, Staunton Smith & Johnson 1995) whereas guano-N is dominated by uric acid (50 to 80%). The other major N-containing compound in guano is NH_4^+, making up 8 to 40%, while amino acids and proteins occur in smaller amounts (Lindeboom 1884, Schmidt et al. 2004). After guano deposition on the island, ammonia volatilizes rapidly from the uric acid and causes 25 to 80% losses of total guano-N (Lindeboom 1884, Staunton Smith & Johnson 1995). In water, nutrients from the guano are rapidly dissolved, and most dissolved N occurs as NH_4^+ (Loder et al. 1996).

In the present study, we utilized 18 islands: 7 active cormorant islands with various nest densities, 2 recently abandoned cormorant nesting islands, and 9 islands without nesting cormorants (Table 1). Among these islands, 12 were located in the northern part of the archipelago (59° 30′ to 41′ N, 18° 32′ to 19° 02′ E) and 6 in the southern part (58° 52′ to 59° 06′ N, 17° 54′ to 18° 21′ E) (Fig. 2). Because our previous data indicated that ornithogenic nitrogen only enters surrounding waters in detectable amounts at high nest densities (Kolb et al. 2010), we grouped the active cormorant island into 2 categories according to their nest density: 3 islands with a low (<0.03 nests m^{-2}) and 4 islands with a high (>0.03 nests m^{-2}) nest density. When selecting reference islands, we chose islands in the

same range of size, distance to the mainland, wave exposure, and vegetation structure as the cormorant islands, to reduce the probability of confounding results (Table 1). Cormorants are sensitive to human disturbance, and colonies in the Stockholm archipelago are typically established on islands with limited activity (R. Staav pers. comm.). No other island characteristics predicted cormorant presence or nest density. Wave exposure was calculated as effective fetch (distance of free water) in 16 directions for each sample sides with the help of the program Wave-Impact (Isæus 2004) (Table 1). We excluded one active cormorant island (Våmkubben) with a high nest density from the statistical analyses because its unusual topography made bottom-up effects from cormorants on the focal species extremely unlikely. Våmkubben is a very steep and exposed island, and the cormorant colony is concentrated on a side without a *Fucus* belt. Because of the steep slope, the runoff is concentrated on this side, and the side with the *Fucus* belt can be expected to receive only a small amount of the nutrient runoff that is rapidly dispersed due to the high wave exposure. Comparison of algal $\delta^{15}N$ ratios from Våmkubben with reference islands, having similar wave exposure, supported our assumption that only a very low concentration of ornithogenic N was dissolved in the water around the *Fucus* belts of Våmkubben. *Fucus* from Våmkubben were depleted in ^{15}N ($\Delta\delta^{15}N = -3.5$), and epiphytic algae were only slightly enriched ($\Delta\delta^{15}N = 3.0$).

Fucus vesiculosus is the most common and widespread canopy-forming species in the Baltic Sea and is considered to have an important function as habitat for a number of invertebrate species. During the last decades, *Fucus* has declined strongly (Malm & Isæus 2005). This decline has been explained among others by indirect effects of eutrophication (e.g. Worm et al. 2000, Berger et al. 2003). In the present study, the most common epiphytic algae associated with *Fucus* were the brown algae *Ectocarpus siliculosus* and *Elachista fuciola*, the red algae *Ceramium* spp., and the green algae *Enteromorpha* spp. and *Cladophora* spp. Generally, algae take up N mainly as ammonium and nitrate, but for many algae ammonium is the preferred inorganic N source (Takamura & Iwakuma 1991, Lobban & Harrison 1994).

The most abundant grazers associated with *Fucus* were the mollusc *Theodoxus fluviatilis*; the crustaceans *Jaera albifrons*, *Gammarus* spp. and *Idotea* spp.;

Table 1. Characteristics of 18 islands studied (cormorant nesting islands and reference [i.e. non-cormorant] islands) in the Stockholm archipelago, Baltic Sea. Locations are shown in Fig. 2. Wave exposure was calculated as effective fetch (distance of free water) in 16 directions for both *Fucus* sample sides (A & B) for each island with the help of the program WaveImpact (Isæus 2004)

Location	Island (nest m^{-2})	Active nest density	Island category	Wave exposure
1	Marskärskobben	0.025	Active with low nest density	A 19060; B 18821
1	Fårörarna	0	Reference	A 21710; B 21710
2	Stora Träskär	0	Abandoned	A 52051; B 51900
2	Stora Halmören	0	Abandoned	A 51374; B 50072
2	Västra Mellgrund	0	Reference	A 50567; B 50393
2	Ägglösen	0	Reference	A 71649; B 77045
3	Bergskärit	0.029	Active with low nest density	A 16834; B 19002
3	Mjölingsören	0	Reference	A 17361; B 17361
4	Nickösören	0	Reference	A 9793; B 9783
4	Hannaholmen	0	Reference	A 7616; B 8023
4	Norra Ryssmasterna	0.039	Active with high nest density	A 9524; B 9202
4	Norra Småholmen	0.063	Active with high nest density	A 6785; B 7738
5	Fredagen	0	Reference	A 11073; B 10883
5	Skraken	0.024	Active with low nest density	A 8846; B 8613
6	Våmkubben	0.041	Active with high nest density	A 340983; B340983
6	Rödkläppen	0	Reference	A 382085; B388320
6	Fälöv	0.034	Active with high nest density	A 181913; B 180627
6	Skorvan	0	Reference	A 297421; B 298047

and Chironomidae (insect). Here we focused on these 5 taxa because they are all known to feed at least partly on *Fucus* or its epiphytic macro- and microalgae (Sjöberg 1967, Goecker & Kall 2003, Korpinen et al. 2008). *J. albifrons* grazes on microalgae, bacteria, and macroalgae (Sjöberg 1967, Pavia et al. 1999). *T. fluviatilis* is a scraper feeding primarily on periphyton (Liess & Haglund 2007), whereas *Gammarus* spp. and *Idotea* spp. are shredders (Schwoerbel 1993) feeding mostly on macroalgae in the Baltic Sea (Goecker & Kall 2003). Chironomidae is a species-rich family that, in the Stockholm archipelago, is dominated by herbivores and detritivores (Y. Brodin pers. comm.).

Sampling. We located *Fucus* belts by snorkelling around the islands, within 1 to 4 m from the shoreline. We chose 2 representative sample sites per island, if possible on opposite island sides. We randomly collected 6 *Fucus* fronds per island, 3 fronds per sample site. On 4 islands, an extra *Fucus* frond was collected to ensure a sufficient number of invertebrate samples for stable isotope analysis. Samples were collected 0.5 to 5 m from the shoreline, and at 0.5 to 2 m depth. We used a 0.2 m^2 frame with an attached net bag (1 mm mesh size) to collect samples from a standardized area (Råberg & Kautsky 2007). Samples were immediately transferred into plastic bags and stored in the freezer until sorting. In the laboratory, samples were sorted; invertebrates (>1 mm) were identified to family, genus, or species level and counted. *Theodoxus fluviatilis*, *Gammarus* spp. and *Idotea* spp. were divided into 3 size classes. For each island, subsamples of about 100 individuals of each taxon and

size class were dried at 55°C to constant dry-weight and weighed. Based on the subsamples, mean island individual dry weights for each taxon and size class were used in combination with the abundance data to estimate the total biomass (measured as dry weight) for each taxon and *Fucus* sample. To calculate the ratio of epiphytic algae to *Fucus* in each sample, one branch of the *Fucus* frond was cleaned from all epiphytic algae by scraping. The uncleaned *Fucus* fronds, epiphytic-free *Fucus,* and the epiphytic algae were dried (55°C) and weighed.

Stable isotope and nutrient content analysis. For stable isotope, N, and P content analysis, per *Fucus* frond, one sample from the young *Fucus* tips and from the major epiphytic algae of the *Fucus* frond were used. The *Fucus* samples were cleaned from epiphytes prior to analysis. For stable isotope and nitrogen analysis, 5 to 6 *Fucus* fronds were used per island, whereas for the phosphorus analysis only 2 fronds were used, one from each sampling side. The stable isotope signature and N content analyses were conducted for all 5 invertebrate groups. For each group up to 6 samples, if possible one sample per *Fucus* frond was analyzed per island. Individuals belonging to larger size classes were preferred in this analysis. If possible, animal specimens were analyzed individually, and only legs were used to avoid gut contents, but pooled samples of whole bodies were used for Chironomidae and *Jaera albifrons* because of their small individual weight (< 0.7 mg). *Theodoxus fluviatilis* was removed from its shell, and only the soft body was used for analysis. Animals were freeze-dried and algae oven-dried (55°C) prior to analysis.

Phosphorus content (%P, dry mass basis) was assayed using persulphate digestion and ascorbate-molybdate colorimetry (Clesceri et al. 1998). The stable isotope ratios for C and N and nitrogen content were measured in an isotope ratio mass spectrometer (Europa Scientific Integra). Isotope ratios were calculated as deviations from the international limestone standard Vienna PeeDee Belemnite (VPDB) (δ^{13}C) and from atmospheric N (δ^{15}N) in parts per thousand (‰):

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is the heavier isotope of the element (^{13}C or ^{15}N) and R is the isotopic ratio (^{13}C/^{12}C or ^{15}N/^{14}N).

The stable isotope signature (δ^{13}C and δ^{15}N) of primary producers is constrained by their habitat, their carbon and nitrogen source, their biochemical structure, and the photosynthetic mechanism (Fry 2006).
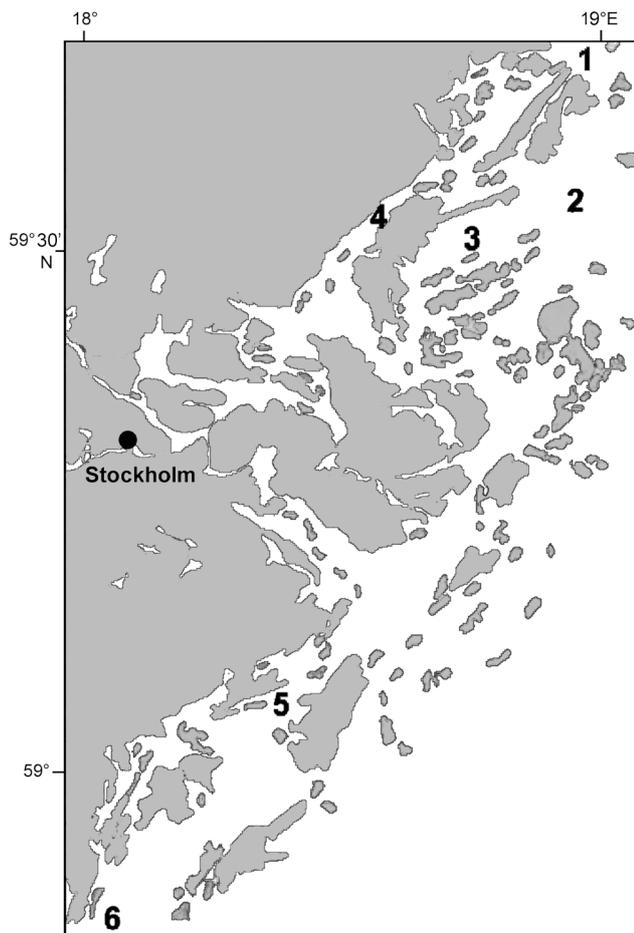

Fig. 2. Study areas in the Stockholm archipelago, Baltic Sea. (1) Marskärskobben and Fårörarna; (2) Stora Träskär, Stora Halmören, Västra Mellgrund, and Ägglösen; (3) Bergskärit and Mjölingsören; (4) Nickösören, Hannaholmen, Norra Ryssmasterna, and Norra Småholmen; (5) Fredagen and Skraken; and (6) Våmkubben, Rödkläppen, Fälöv, and Skorvan. Island characteristics are shown in Table 1

The δ^{13}C and δ^{15}N signature of consumers is mainly constrained by their trophic level and diet; isotopic signatures typically reflect the isotope composition of food sources with some predictable changes (fractionation). While δ^{13}C generally changes little between trophic levels, δ^{15}N shows a more distinct increase (McCutchan et al. 2003, Vanderklift & Ponsard 2003). Fish-eating seabirds have enriched δ^{15}N signatures because of the marine diet and their high trophic position (Barrett et al. 2005), and seabird guano is often even more enriched in ^{15}N. This enrichment results from the rapid mineralization of uric acid, the main nitrogen content of guano, to ammonium (NH$_4$). The volatilization is accompanied by a large isotopic fractionation, leaving the remaining NH$_4$ strongly enriched in the heavier ^{15}N (Lindeboom 1984, Mizutani et al. 1986, Wainright et al. 1998). Primary producers taking up this enriched nitrogen from seabird guano therefore have enriched δ^{15}N ratios (Wainright et al. 1998). Consumers feeding on isotopically enriched primary producers also show distinguishably higher δ^{15}N signatures (Barrett et al. 2005). δ^{15}N can therefore be used to demonstrate the importance of avian nitrogen in food webs in and around seabird islands.

Statistical analyses. To investigate if algae and associated invertebrates near cormorant colonies incorporate ornithogenic N in their tissue, we compared stable isotope ratios (δ^{13}C and δ^{15}N) among the 3 groups of cormorant islands and the reference islands using linear mixed effects models. Carbon and nitrogen isotope signatures were analyzed separately, with island category, adjusted wave exposure, and their interaction as fixed effects and islands as random effect. We excluded factors that did not contribute to the model (p > 0.05). In order to meet the assumption of normality and homoscedasticity, we used adjusted wave exposure (i.e. the difference between wave exposure of the sample side and mean wave exposure [wave exposure log-transformed]) in all models. We included wave exposure as covariate because of its great variation between islands studied (Table 1), its effect on nutrient dispersal, and its likely effect on algae and invertebrate community structure (Bustamante & Branch 1996, Eriksson et al. 2004).

Based on the δ^{13}C and δ^{15}N ratios (island mean ± SD) of *Fucus* and epiphytic algae, we estimated the relative proportion of these food sources in the diet of 5 aquatic invertebrates with the software MixSIR (Moore & Semmens 2008). MixSIR is a Bayesian mixing model that estimates probability distributions of source contributions to a mixture while explicitly accounting for uncertainty associated with multiple sources, fractionation, and isotope signatures (Moore & Semmens 2008). MixSIR estimates not only the predicted proportion of food sources in the diet but also confidence

intervals of these estimates. Means of different taxa were considered different when they were not included in the 95% confidence interval of the other group.

Before applying the diet mixing models, we standardized the lipid content of the samples (both sources and consumers) with a mathematical normalization technique (Post et al. 2007). This technique normalizes the $\delta^{13}C$ ratio of a sample for its lipid content by using the C:N ratios for animals and the %C content for plants. The approach is based on the strong relationship between (1) C:N ratio of animals and their lipid content, (2) the C content of plants and their lipid content, and (3) the lipid content and the change in $\delta^{13}C$ ($\Delta\delta^{13}C$) (Post et al. 2007). The specific equations used were:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$$
for aquatic invertebrates

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.02 + 0.09 \times \%C$$
for plants with C < 40%

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 5.83 + 0.14 \times \%C$$
for plants with C > 40%

We calculated estimates of the carbon and nitrogen fractionation factors ($\delta^{13}C$ and $\delta^{15}N$) from the isotopic ratio of the 2 sources (*Fucus* and epiphytic algae) for each consumer by using the equations by Caut et al. (2009):

$$\delta^{13}C = -0.11\ \delta^{13}C - 1.92$$
$$\delta^{15}N = -0.31\ \delta^{15}N + 4.06$$

Diet mixing models were analysed with both untreated $\delta^{13}C$ ratios and lipid-normalized $\delta^{13}C$ ratios because it remains unclear if this normalization is necessary (Post et al. 2007), especially for aquatic invertebrates (Logan et al. 2008). While many studies using stable isotope analysis ignore lipid effects totally (Vander-Zanden & Rasmussen 1999), other studies show strong effects of lipid-normalization on the

results of diet mixing models (Kiljunen et al. 2006). By using a 2-source isotope mixing model including *Fucus* and epiphytic algae, we ignored other possible food sources like microalgae and bacteria. *Theodoxus fluviatilis* mainly feed on periphyton (Liess & Haglund 2007), and our analysis might therefore be less useful for identifying diet changes for this species.

Linear mixed effects models were also used to test for differences in (1) the epiphytic algae to *Fucus* ratio, (2) nitrogen and phosphorus content of algae and invertebrate, (3) abundance, and (4) biomass of the 5 invertebrate groups between reference islands and the 3 cormorant island categories. Island category, adjusted wave exposure, and their interaction were used as fixed factors in this analysis, with island as random factor. In order to meet the assumption of normality and homoscedasticity, we transformed the response variables: epiphytic algae to *Fucus* ratio and invertebrate biomass (i.e. dry-weight invertebrates [mg] per dry-weight algae (*Fucus* and epiphytic algae) [g]) were square-root transformed, whereas invertebrate abundance (i.e. individuals per g dry-weight algae) was log transformed. All linear mixed effect models were performed using the nlme package in R.2.9.2 (R Development Core Team 2007).

RESULTS

Stable isotope and nitrogen content analyses

Stable isotope analyses showed that all algae and consumers collected nearby active cormorant islands with high nest densities were strongly enriched in $\delta^{15}N$ compared with reference islands (Fig. 3, Table 2). *Fucus*, epiphytic algae, and Chironomidae were more enriched in $\delta^{15}N$ ($\Delta\delta^{15}N$ = 11.3 to 11.7) than *Gammarus* spp., *Idotea* spp. *Jaera albifrons* and *Theodoxus fluviatilis* ($\Delta\delta^{15}N$ = 7.2 to 8.1). Near islands with low nest densities, algae (*Fucus*: $\Delta\delta^{15}N$ = 3.4 and epiphytes:
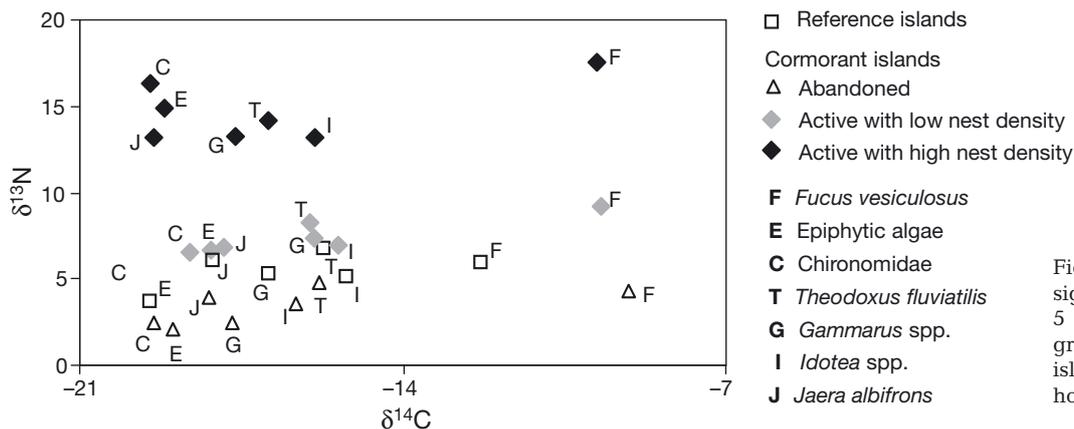

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ signatures of algae and 5 aquatic invertebrate groups from different islands in the Stockholm archipelago, Baltic Sea

☐ Reference islands

Cormorant islands
△ Abandoned
◆ Active with low nest density
◆ Active with high nest density

F *Fucus vesiculosus*
E Epiphytic algae
C Chironomidae
T *Theodoxus fluviatilis*
G *Gammarus* spp.
I *Idotea* spp.
J *Jaera albifrons*

Table 2. Results of linear mixed effect models (lme) testing for differences in the δ^{15}N signatures of algae and aquatic invertebrate groups between reference islands (i.e. noncormorant) and 3 categories of cormorant islands (abandoned, active with low and high nest densities). Samples were collected in the surrounding water bodies of 17 islands in the Stockholm archipelago, Baltic Sea. den df: denoted df.

Note: Results from ANOVA table for lme are shown

Taxon	den df	*F*	p	Slope (mean ± SE)
Fucus vesiculosus	84			
Island category	13	28.1	<0.0001	
Wave exposure	84	3.1	0.082	−0.7 ± 0.4
Epiphytic algae	136			
Island category	13	38.7	<0.0001	
Wave exposure	136	8.9	0.004	−0.9 ± 0.3
Chironomidae	73			
Island category	13	28.6	<0.0001	
Wave exposure	73	3.5	0.066	−1.0 ± 0.4
Theodoxus fluviatilis	60			
Island category	11	14.8	<0.001	
Wave exposure	60	5.0	0.030	−1.0 ± 0.5
Gammarus spp.	103			
Island category	13	11.9	<0.001	
Wave exposure	103	5.7	0.019	−1.0 ± 0.5
Idotea spp.	124			
Island category	13	11.1	<0.001	
Wave exposure	124	10.4	0.002	−1.2 ± 0.4
Jaera albifrons	50			
Island category	11	17.9	<0.001	
Wave exposure	50	4.8	0.033	−0.9 ± 0.4

Fig. 4. Percent consumption of epiphytic algae (epiphyte) (median ± 95% CI) of aquatic invertebrate groups collected in coastal waters of reference islands (n = 9), abandoned cormorant islands (n = 2), and active cormorant islands with low (n = 3) and high (n = 3) nest density in the Stockholm archipelago, Sweden. Percent consumption was calculated with diet mixing models (MixSIR). (A) Untreated δ^{13}C ratios were used for the models. (B) Lipid-normalized δ^{13}C ratios were used for the models (Post et al. 2007)

$\Delta\delta^{15}$N = 2.8) but not consumers showed a tendency towards a slight δ^{15}N enrichment (Fig. 3, Table 2). All groups showed or tended to show decreasing δ^{15}N signatures with an increasing wave exposure (Table 2). *T. fluviatilis* was depleted in δ^{13}C nearby cormorant islands with a high nest density ($\Delta\delta^{13}$C = −1.2, den df (denoted df) = 11 and 60, *F* = 2.6, p = 0.10), and *J. albifrons* showed a similar tendency ($\Delta\delta^{13}$C = −1.3, den df = 11 and 51, *F* = 1.8, p = 0.20). *T. fluviatilis* tended to have increasing $\Delta\delta^{13}$C signatures with an increasing wave exposure (*F* = 3.4, p = 0.07). The interaction island type × wave exposure did in no case contribute significantly to isotope variation.

Both diet mixing models, with untreated δ^{13}C ratios (model I) or with lipid-normalized δ^{13}C ratios (model II), indicated that all consumers except Chironomidae tended to higher relative consumption of epiphytic algae near active cormorant islands with high nest density compared to reference islands, but the tendency was more pronounced in model II (Fig. 4). Such an increased consumption of epiphytes was also found for *Theodoxus fluviatilis*, *Idotea* spp. (both models), and *Gammarus* spp. (only model I). Near cormorant islands with low nest densities and abandoned cor-
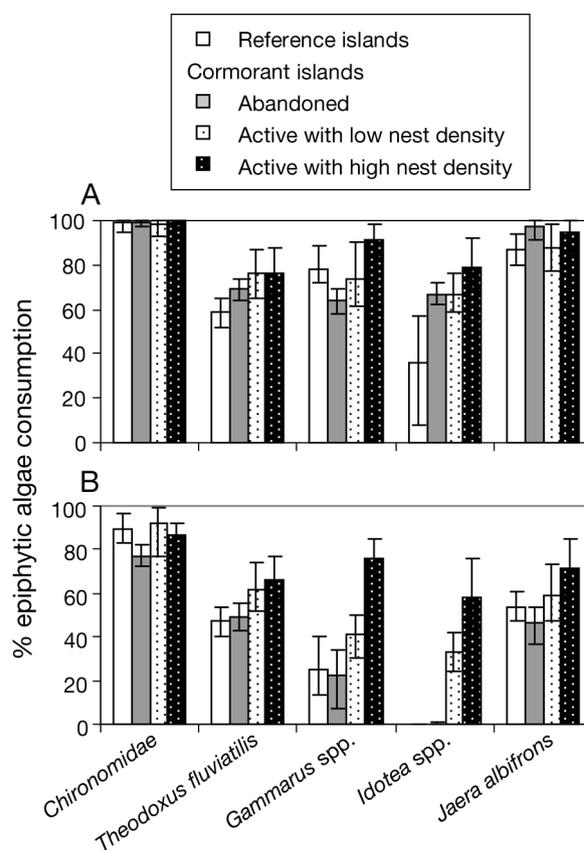
morant islands, the pattern was less clear and differed between the models and among taxa (Fig. 4). Generally, model I predicted a higher percentage epiphyte consumption than model II. However, both models indicate that *Idotea* spp. was the group with the highest degree of *Fucus* feeding, whereas Chironomidae was the group with the lowest degree of *Fucus* feeding (Fig. 4).

Fucus and epiphytic algae around cormorant islands with a high nest density had 61% and 57%, respectively, higher N content than algae around reference islands (Fig. 5, Table 3). Of the 5 invertebrate groups, only *Idotea* spp. had a higher N content (15%) near islands with high nest densities than near reference islands (Fig. 5, Table 3). There were no differences in N content for any group between islands with a low nest density and reference islands. *Gammarus* spp. tended towards lower N content near abandoned cormorant islands compared to reference islands (Fig. 5, Table 3). The N con-
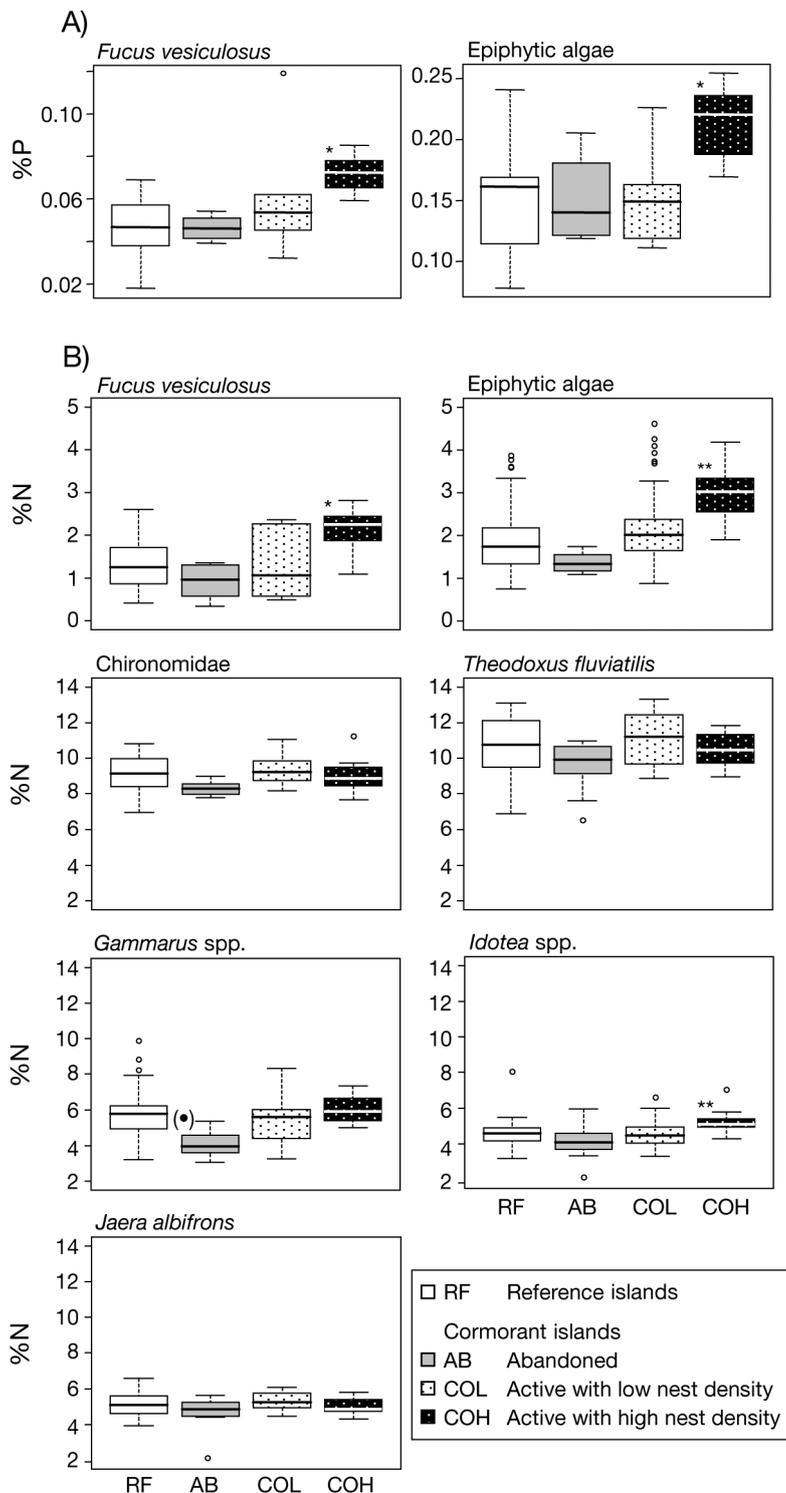
Fig. 5. (A) Phosphorus content of algae and (B) nitrogen content of algae and aquatic invertebrate groups collected in coastal waters of 4 island categories in the Stockholm archipelago, Baltic Sea. Shown are median values of the response variable with upper box showing 75th percentile, lower box showing 25th percentile, and whiskers showing values within the range of 1.5 interquartile distances. (•) $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ refer to level of significance for difference in N and P content relative to reference islands

tent of Chironomidae was negatively correlated to wave exposure, and epiphytic algae tended towards the same negative correlation (Table 3). There was a significant interaction between island category and wave exposure for the N content of *Jaera albifrons*, which was due to a negative correlation with wave exposure near reference islands but slightly positive correlation near active cormorant islands with high nest density. Also the P content of *Fucus* (54% higher) and epiphytes (45% higher) was higher nearby active cormorant islands than reference islands (Fig. 5, Table 3).

Fucus growing near cormorant islands with high nest density had 64% more epiphytic algae than *Fucus* nearby reference islands (den df = 13 and 85, F = 4.0, p = 0.033) (Fig. 6). The epiphytic algae to *Fucus* ratio near active cormorant islands with a low nest density and near abandoned cormorant islands did not differ from the ratio near reference islands. Exposure did not affect the ratio.

Invertebrate abundance and biomass

Cormorant colonies with high nest densities affected the abundance of one and tended to do so of 2 out of 5 investigated aquatic invertebrate groups. *Jaera albifrons* was 2.6-fold more abundant around active islands with high cormorant nest densities than around reference islands. Chironomidae and *Gammarus* spp. tended to have a 3.2-fold and 3.4-fold higher abundance around high nest density islands than around reference islands (Fig. 7A, Table 4). The abundances of *Theodoxus fluvi-*
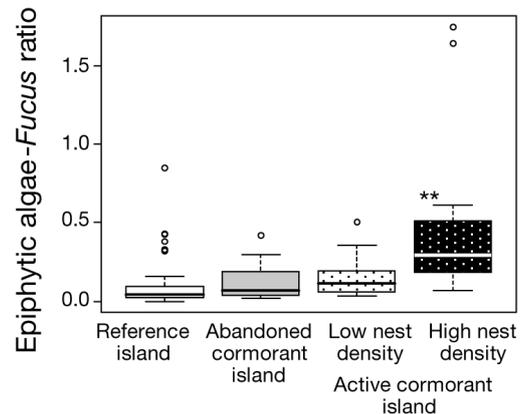

Fig. 6. Epiphytic algae:*Fucus* ratio of algae collected in coastal waters of 4 island categories in the Stockholm archipelago, Baltic Sea. See Fig. 5 for further explanations

Table 3. Results of linear mixed effects model (lme) testing for differences in nitrogen (%N) and phosphorus (%P) content of algae and aquatic invertebrate groups between reference (RF) (i.e. non-cormorant islands) and 3 categories of cormorant islands (abandoned [AB], active with low [COL] and with high [COH] nest densities). Samples were collected in water bodies surrounding 17 islands in the Stockholm archipelago, Baltic Sea. Note: ANOVA tables for lme are shown; when the interaction between island category and wave exposure was significant, wave exposure slopes are given for reference islands and island categories with a slope significant different to reference islands

Taxon	den df	F	p	Slope (mean ± SE)
% N				
Fucus vesiculosus	85			
Island category	13	4.1	0.030	
Epiphytic algae	136			
Island category	13	6.2	0.008	
Wave exposure	136	3.1	0.083	−0.1 ± 0.1
Chironomidae	73			
Island category	13	0.3	0.811	
Wave exposure	73	12.4	0.001	−0.4 ± 0.1
Theodoxus fluviatilis	61			
Island category	11	0.8	0.538	
Gammarus spp.	47			
Island category	13	1.7	0.224	
Idotea spp.	125			
Island category	13	3.9	0.033	
Jaera albifrons	47			
Island category	11	0.6	0.641	
Wave exposure	47	37.8	<0.0001	RF: −0.8 ± 0.1 AB: 1.0 ± 0.2 COH: 1.0 ± 0.3
Island × Wave	47	9.0	<0.0001	
% P				
Fucus vesiculosus	17			
Island category	13	3.0	0.070	
Epiphytic algae	18			
Island category	12	3.1	0.068	

Table 4. Results of linear mixed effect models testing for differences in abundance (individuals per g dry-weight algae) (log[x + 0.5] transformed) and biomass (mg dry-weight invertebrates per g dry-weight algae) (square root transformed) of algae and aquatic invertebrate groups between reference (RF) (i.e. non-cormorant) islands and 3 categories of cormorant islands (abandoned [AB], active with low [COL] and high [COH] nest densities). Samples were collected in the surrounding water bodies of 17 islands in the Stockholm archipelago, Baltic Sea. See Table 3 for further explanations

Taxon	den df	F	p	Slope (mean ± SE)
Abundance				
Chironomidae	85			
Island category	13	1.3	0.331	
Theodoxus fluviatilis	84			
Island category	13	1.9	0.176	
Wave exposure	84	20.6	<0.0001	−0.33 ± 0.07
Gammarus spp.	85			
Island category	13	1.4	0.295	
Idotea spp.	85			
Island category	13	2.5	0.109	
Jaera albifrons	81			
Island category	13	2.8	0.082	
Wave exposure	81	6.7	0.012	RF: −0.3 ± 0.1 COH: −0.6 ± 0.2
Island × Wave	81	3.1	0.033	
Biomass				
Chironomidae	81			
Island category	13	2.5	0.057	
Theodoxus fluviatilis	84			
Island category	13	2.7	0.089	
Wave exposure	84	21.9	<0.0001	−1.2 ± 0.3
Gammarus spp.	81			
Island category	13	7.6	0.004	
Wave exposure	81	0.6	0.458	RF: −0.2 ± 0.2 COH: −1.7 ± 0.4
Island × Wave	81	6.4	0.001	
Idotea spp.	85			
Island category	13	0.6	0.602	
Jaera albifrons	81			
Island category	13	5.6	0.011	
Wave exposure	81	13.2	0.001	RF: −0.1 ± 0.0 COH: −0.2 ± 0.0
Island × Wave	81	5.2	0.002	

atilis and *J. albifrons* around reference islands and active cormorant islands with high nest density were negatively correlated with wave exposure (Table 4). The biomasses of *J. albifrons*, *Gammarus* spp., and Chironomidae were greater near islands with high nest densities than near reference islands. Near high nest density islands, Chironomidae had 5.6-fold, *Gammarus* spp. 1.8-fold, and *J. albifrons* 1.4-fold higher mean dry-weight per dry-weight algae than near reference islands (Fig. 7B, Table 4). There was a significantly interactive effect between island type and wave exposure for *J. albifrons* abundance and biomass and the biomass of *T. fluviatilis* and *Gammarus* spp., and this interaction was due to a more negative correlation with wave exposure around high nest density islands than around reference islands (Table 4).

DISCUSSION

Seabirds can strongly affect the island ecosystem by fertilizing soils and subsidizing several trophic levels (Polis & Hurd 1995, Ellis 2005, Towns et al. 2009). Our results showed, similar to earlier studies (Golovkin 1967, Bosman & Hockey 1988, Wootton 1991, Lapointe et al. 1992), that seabirds affect not only the terrestrial ecosystem but also aquatic primary producers and their consumers near nesting islands. However, strong effects on algae and invertebrates were only observed near islands with a high nest density. In our system,
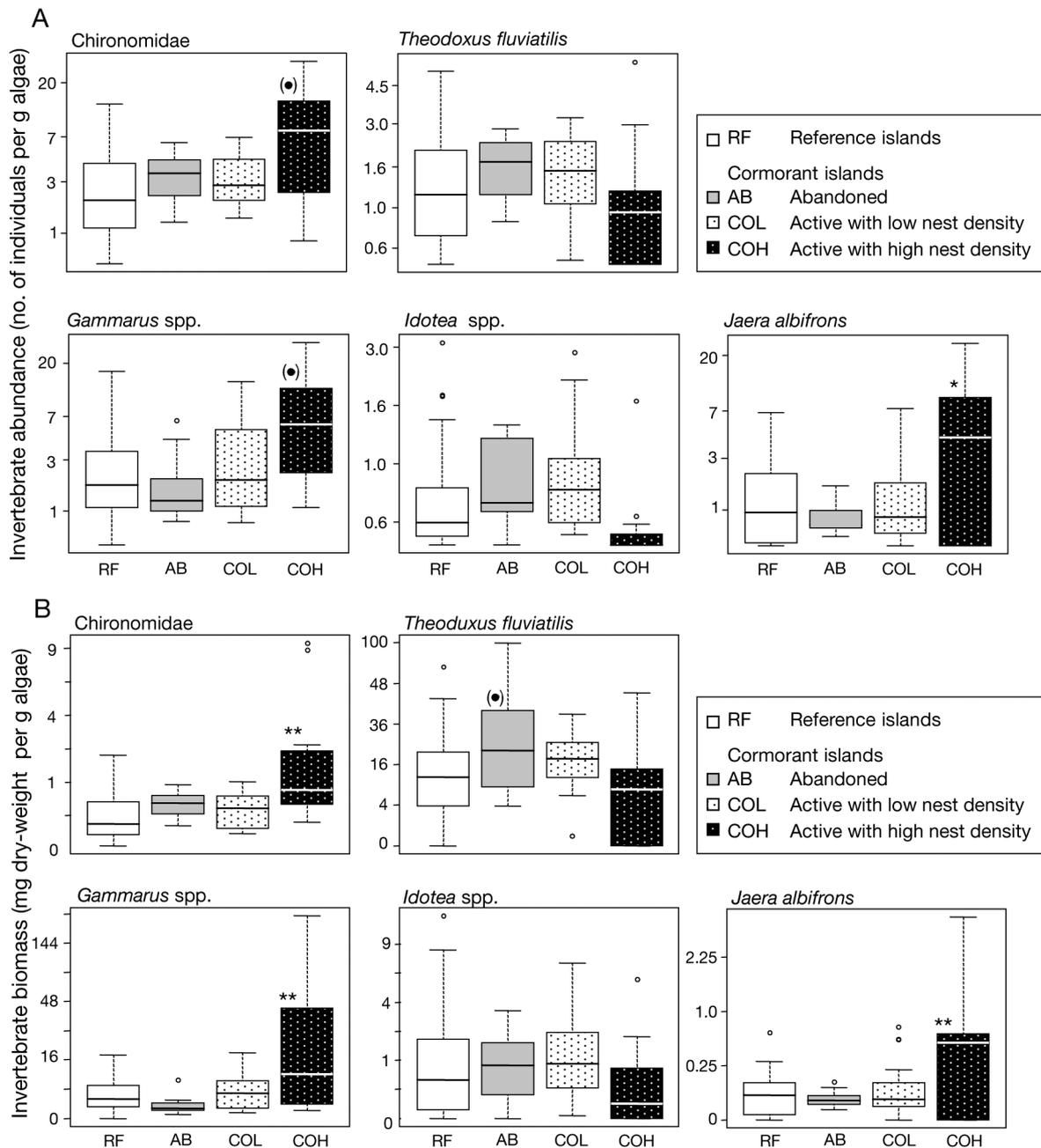
Fig. 7. (A) Abundance and (B) biomass of marine invertebrates (number of individuals per g dry-weight algae) collected in water bodies surrounding 4 island categories (reference islands [RF], abandoned cormorant islands [AB], active cormorant islands with low [COL] and high [COH] nest density) in the Stockholm archipelago, Baltic Sea. (A) Scale is log-transformed; (B) scale is square-root transformed. See Fig. 5 for further explanations

ornithogenic N and P probably enter the surrounding water mainly via runoff and, in smaller amounts, via direct guano excretion into the water and in rain-dissolved ammonia, and significant runoff will likely only occur from islands with high nest density. The vegetation on islands with low nest density is probably able to take up most of the non-volatilized guano-N (Kolb et al. 2010), and most P will be taken up or bound in the soils on these islands. Increased nutrient con-

centrations (NH_4^+, NO_3^-, NO_2^- and PO_4^-) in adjacent waters have been reported from other high nest density seabird islands (Bosman et al. 1986, Lapointe et al. 1992). However, nutrient concentration in waters surrounding seabird islands might not only depend on nest density but also on island structure and vegetation, wave exposure, and weather conditions (Loder et al. 1996, Young et al. 2011). Strong rains will flush much dry guano from the islands into the water and

thus increase water nutrient concentration, whereas high temperatures and sunshine will increase volatilization of NH_3 from the water and thus decrease N concentrations (Loder et al. 1996).

Seabird islands with a high nest density and a low wave exposure may be seen as a natural experiment for studying the effects of eutrophication on marine communities. We found, consistent with former fertilisation experiments, increased algal nitrogen and phosphorus content and a higher epiphytic algae to *Fucus* ratio on cormorant islands with an increased nutrient availability (Pedersen & Borum 1996, Worm et al. 2000, Kraufvelin et al. 2006, Kraufvelin 2007, Råberg & Kautsky 2008). Contrary to previous studies investigating the effect of nutrient enrichment, on grazers in the Baltic Sea (Kotta et al. 2000, Worm & Sommer 2000, Kraufvelin et al. 2006, Kraufvelin 2007, Korpinen et al. 2010) and chironomids in Lake Michigan, USA (Blumenshine et al. 1997), not all invertebrates responded with increased abundance. Among the 5 invertebrate groups, only *Jaera albifrons* showed significantly higher density and biomass near cormorant islands with high nest densities. *Gammarus* spp. and Chironomidae similarly showed increased biomass, but the effect on density was non-significant. The different responses in biomass and abundance can be explained by a changed species composition towards larger species or larger-bodied individuals of the same species. A shift towards larger species in response to water nutrient enrichment has been reported for Chironomidae but not for Gammaridae (Blumenshine et al. 1997). Furthermore, all identified *Gammarus* species (*G. oceanicus*, *G. zaddachi*, *G. salinus*, and *G. locusta*) in our samples have about the same size (Barnes 1994). This indicates that the biomass increase of *Gammarus* spp. near cormorant islands with a high nest density was caused by increased individual body sizes.

Surprisingly, neither *Idotea* spp. nor *Theodoxus fluviatilis* showed increased abundances or biomasses near cormorant colonies. This pattern was unexpected considering (1) that *Idotea* have been shown to prefer filamentous algae over *Fucus* as food source (Karez et al. 2000, Goecker & Kåll 2003, Orav-Kotta & Kotta 2004, but see also Jormalainen et al. 2001); (2) the positive relationships between epiphyte loads and grazer densities (Kotta et al. 2000, Worm & Sommer 2000); (3) that *Idotea baltica* exhibited increased growth rate, egg size, and number when feeding on nitrate, ammonia, and phosphate-fertilized *Fucus* (Hemmi & Jormalainen 2002); and (4) the general importance of nitrogen as a limiting factor for invertebrates (Mattson 1980, Elser et al. 2000). An explanation for the lack of response of *Idotea* spp. might be the role that *Fucus* plays as a habitat, providing not only food but also shelter against disturbance or predation (Orav-Korra

& Kotta 2004, Wikström & Kautsky 2007, Råberg & Kautsky 2007). *Idotea* spp. is the largest-bodied genus among the investigated invertebrates. They are, with a dorsiventrally flattened body, well adapted to the large, tough branched *Fucus*. Therefore, they might be more dependent on *Fucus* as a shelter than the smaller *Jaera albifrons*, *Gammarus* spp. and Chironomidae. Furthermore, the isotopic diet mixing model indicated that *Idotea* spp. did not prefer epiphytic algae as a food source as strongly as the other invertebrates and had a relatively higher *Fucus* consumption. Our results from the diet mixing model are of particular interest considering that previous studies on the diet preference of invertebrates of the Baltic Sea rarely utilized stable isotope analysis and furthermore disagree in the preferred diet source of *Idotea* (Karez et al. 2000, Jormalainen et al. 2001, Goecker & Kåll 2003). *T. fluviatilis* might, similarly to *Idotea* spp., suffer from decreased shelter but also from the increased filamentous algae load that competes with microalgae, an important food source for the scraping snails (Råberg & Kautsky 2008).

The present study focused on the possible bottom-up effect of cormorants on producers and consumers in coastal waters surrounding their nesting islands and disregarded possible top-down effects of cormorants through fish consumption. Top-down effects from seabirds on several trophic levels have been observed in intertidal zones, in which seabirds prey on limpets, snails, and crabs (Ellis et al. 2007, Wooten 1992, Kurle et al. 2008), but it is debatable to what extent fish-eating seabirds affect their prey populations (Draulans 1988). Most seabirds forage in large marine areas and share their prey with other predators (e.g. fishery, mammals, and predatory fishes), which makes it difficult to study their effect on the abundance of their prey and lower trophic levels. However, several studies have investigated the effect of cormorants, with differing results; but all studies are from rather closed aquatic systems with a clear separation between within an outside cormorant foraging range (Birt et al. 1987, Engström 2001, Lehikoinen 2005, Dalton et al. 2009). Similar studies are difficult in our more open study system since reference islands lay within the feeding range of cormorants. Furthermore, we only studied the effect of cormorants in coastal waters (>5 m distance from the shore line) and thus were not able to make any prediction about the size of the area affected by ornithogenic nutrients. However, we found in an unpublished study that aquatic vascular plants and algae showed enriched $\delta^{15}N$ ratios within 30 m of an active cormorant island with high nest density. Certainly wave exposure and water depth might also play important roles in determining the size of the impact zone, but our results nevertheless show that nesting cor-

morants can affect algae and some invertebrates in coastal waters; however, additional studies are needed to understand if invertebrates mainly responded to the increased epiphytic algae load, the increased algal nitrogen content, or the increased algal phosphorus content.

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